

SEED BANKS OF LONG-UNBURNED STANDS OF
MARITIME CHAPARRAL: COMPOSITION, GERMINATION BEHAVIOR,
AND SURVIVAL WITH FIRE

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ABSTRACT

Seed germination requirements in the California chaparral have been described mainly from freshly collected seed. However, uncertainties remain because the behavior of seeds in the soil can differ. I studied germination of the seed bank in long-unburned stands of maritime chaparral in central coastal California. I quantified seedlings emerging from soil samples provided with appropriate temperature and moisture conditions following 1) no other treatment, 2) a heat treatment to optimize germination of heat-stimulated species, 3) the same heat with the addition of charred wood, and 4) the burning of chaparral stands prior to collection of samples. I compared germination in these treatments with seedling emergence in the field following fire. I also collected and divided samples into 0–2.5 and 2.5–7.5 cm depth fractions to evaluate abundance of seed at the surface and depth before and after fire.

Seed of one annual had reduced germination following the heat treatment. Seeds of all other species common enough to evaluate statistically were heat tolerant. However, because seeds were found to be mostly near the surface, there was considerable mortality with fire. Moreover, seedling populations in the field only accounted for a fraction of the seed bank that survived fire, and seventeen species that germinated in samples did not germinate and/or emerge in the field. Most species' germination and emergence was influenced in some way by heat and/or charate. Germination of two *Ceanothus* was dependent on heat. *Adenostoma fasciculatum* Hook. & Arn., *Arctostaphylos purissima* P. Wells, and two annuals had germination that was enhanced by heat and enhanced further when charate was added. Despite the importance of fire effects, there were no short-lived species having entirely fire-dependent germination. Germination and/or emergence of 3 species was negatively affected by charate. These germinated sparingly or not at all after fire.

One of the most prominent evolutionary specializations to fire exists in the germination ecology of seeds from plants found in Mediterranean shrublands, particularly those of Australia, South Africa, and California (Bond and Van Wilgen 1996). This subject has received considerable attention (Review by Keeley 1991), revealing a fascinating complexity of features that insure germination will coincide with the anomalously favorable conditions for seedling establishment that exist after fire. There are physical features such as bradyspory (or serotiny) where seeds stored in fruits and cones are released when heated by fire (Whelan 1995), and impervious seed coats that open with the heat of fire (Sweeney 1956; Quick and Quick 1961; Auld and O'Connell 1991). Physiologically dormant seed may be induced to grow following fire by chemicals washed from charred wood (Wicklow 1977; Keeley 1984, 1987; Keeley et al. 1985; Keeley and Pizzorno 1986), water soluble nitrogenous compounds (Thanos and Rundel 1996) and smoke (Keith 1997; Keeley and Fotheringham 1997, 1998). For each fire-related germination cue, there are multiple dormancy-releasing mechanisms that have evolved convergently among disparate floras (Baskin and Baskin 1998). In chaparral, germina-

tion without fire may also be inhibited by allelopathic chemicals washed from foliage or litter (Muller et al. 1968; McPherson and Muller 1969), and/or phytotoxins produced by soil microbes (Kaminsky 1981). Fire eliminates these compounds.

Seeds of chaparral plants range from readily germinable at the time of dispersal (non-refractory) to deeply dormant (refractory) as a result of multiple barriers to germination (Keeley and Fotheringham 1998). Some species produce a portion of seed that is refractory and a portion that is not (Emery 1988; Parker and Kelly 1989). Generalizations about the type(s) of dormancy species exhibit derive mainly from tests on freshly collected and stored seed. Germination of seeds residing in the soil may differ significantly, as has been documented for *Adenostoma fasciculatum* Hook. & Arn. and *Arctostaphylos canescens* Eastw. among others (Stone and Juhren 1951; Parker 1987; Keeley and Fotheringham 1998). Seeds exposed to allelopathic chemicals and phytotoxins found in chaparral soils may exhibit enforced dormancy (Muller et al. 1968; McPherson and Muller 1969; Keeley 1991). Therefore, it is imperative to study the soil seed bank to understand how chaparral germination is controlled in nature.

The potential for germination in the chaparral seed bank without fire is thought to be low for most species because seedlings are rarely apparent under

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the shrub canopy. However, Christensen and Muller (1975), Tyler (1995), and Swank and Oechel (1991) reported considerable seedling growth under *Adenostoma* in plots protected from herbivory, suggesting more germination can occur without fire than is evident. In addition, Zammit and Zedler (1988, 1994) and Holl et al. (2000) found that many species germinated readily from chaparral soil seed bank samples. To test how much germination can occur in species' seed banks without fire and how much requires heat and/or chemicals produced by fire, I compared emergence from controls and uniform fire treatments that are known to maximize germination of refractory seed without inducing mortality. I then analyzed how much of the *in situ* seed bank was eliminated above and below 2.5 cm in the soil by fire in the chaparral stands. Finally, I enumerated seedling emergence in the field to compare germination in nature vs. in collected samples.

The chaparral I studied is geographically-isolated and its environment differs in many respects from that found in the Transverse and Peninsular ranges inland. With Santa Ana winds absent, and a lower frequency of ignitions, coastal environments have likely supported less frequent and dynamic fire, at least prior to human dominance of the fire regime (Odion et al. 1992; Odion et al. 1993). The average lifespans of the *Ceanothus* spp. in maritime chaparral are particularly short (Davis et al. 1988) compared to those inland (Keeley 1975, 1992). Death of the non-sprouters opens space for recruitment by numerous herbs and subshrubs (Odion and Davis 2000). These and other factors such as soil and climate may help explain differences in post-fire regeneration in maritime vs. nearby inland chaparral reported by Tyler (1995); they may also have contributed to evolutionary divergence in maritime chaparral taxa that has produced endemic *Arctostaphylos* and *Ceanothus* (Griffin 1978). I have evaluated my germination data for any evidence that the environment and insular nature of the study area manifested variation in germination ecology.

STUDY AREA

Samples were collected from *Adenostoma fasciculatum* (hereafter *Adenostoma*) chaparral located near sea-level, within Vandenberg Air Force Base in central, coastal California as described in D'Antonio et al. (1993), and Odion and Davis (2000). Substratum here is Pleistocene eolian sand (Dibblee 1950). Climate in the area is strongly influenced by the prevailing onshore winds and cool ocean, and the temperature regime is mild, especially for a chaparral environment. Maritime chaparral of the area has been described in detail by Davis et al. (1988). The average annual precipitation is 35.3 cm. I counted annual rings from the obligate seeders, *Arctostaphylos purissima* P. Wells, and *Ceanothus cuneatus* (Hook.) Nutt. var. *fascicularis* (McMinn) Hoover (Keeley 1993) to estab-

lish that the chaparral had not burned for 75–80 y at the site where more intensive sampling was undertaken (site 1). Samples were also collected from a second, nearby site which had not previously burned for about 50 y. Both sites were dominated by *Adenostoma*.

METHODS

Transects consisting of 47 contiguous 1 m² plots were established in dense chaparral dominated by *Adenostoma*. Nine 5 cm diam, 7.5 cm deep cores of soil were obtained per plot at site 1 in the fall of 1988. Five cores were collected in fall, 1989 at site 2. Chaparral at both sites was burned soon thereafter, with low fuel moisture contributing to relatively intense fires (Odion and Davis 2000). I collected 5 cores per plot the day after each fire. Seed bank cores for each plot were composited, and 350 cc subsamples were removed from each homogenized sample.

Pre-burn samples from site 1 were given three treatments: 1) heat, 2) heat and charate (charred, pencil-sized *Adenostoma* stems collected after the fire and ground up) and 3) control (no heat or charate). Only the second of these treatments was used on pre-burn samples from site 2. Samples to be heated were spread to a depth of 2–3 mm on aluminum cooking trays. Based on studies by Wright (1931), Sampson (1944), Sweeney (1956), Keeley and co-workers (several publications, see Keeley (1991), heating at 100°C for ~5 min typically produces the greatest germination response among fire-recruiters, and is well within their heat tolerance. Given the slight insulation the soil would provide, I decided to use a 7 min duration. Heat-induced seed mortality is controlled predominantly by maximum temperature, as opposed to duration (Borchert and Odion 1995), so it is unlikely that this change effected mortality. Heating was done in a forced-air oven.

The subsamples were spread on sterile sand in 20 cm plastic pots. The amount of charate added was 2 rounded tablespoons (21.3 ± 0.94 g, $n = 11$).

The pots were covered with clear plastic, protected from herbivory, and kept moist out-of-doors under 50 percent shade cloth at Cal-Orchid Nursery in Santa Barbara, where temperature fluctuations were analogous to the field. Potting was complete in late November, at which time all samples were given their first watering. All the samples were exposed to outdoor temperatures from the time of collection through the subsequent growing season to provide natural temperature stratification.

Seed bank sampling was also undertaken at randomly located ~1.5 m diam canopy gap areas adjacent to the site 1 transect. I took samples from the center of the gap as well as the edge and understory of the adjacent *Adenostoma* canopy. These cores were separated into 0–2.5 cm and 2.5–7.5 cm

depth fractions and given the heat and charate treatment. Due to smaller amounts available, 175 cc subsamples were spread over sand in 16 cm diam plastic pots placed with the others.

All germinants were identified and removed from pots through the growing season. Nomenclature follows Hickman (1993). Specimens whose identity was uncertain were grown until it was determined. Five of the pre-burn samples treated to heat and charate were removed from pots after emergence stopped. I repotted these the following autumn. No further germination occurred in these.

RESULTS

General patterns. Seed from 72 species germinated and emerged from samples collected along transects (Table 1). More than half (48) were annuals. Site 2 had greater diversity (60 vs. 48 species). Many of the same species emerged abundantly from samples from both sites (e.g., *Adenostoma*, *Helianthemum scoparium* Nutt., *Crassula connata* (Ruíz Lopez & Pavón) A. Berger, *Centaurium davyi* (Jepson) Abrams, and *Navarretia atractylodes* (Benth) Hook & Arn.). Despite this, there were only 33 species in common. In addition, two subshrubs, *Mimulus aurantiacus* Curtis and *Lotus scoparius* (Nutt.) Otley, were abundant in site 2 samples and absent in those from site 1. Several annuals were common in samples from one site but not the other. Nine species were non-native. All 9 are widespread weeds.

Post-burn samples contained 44 species (1 non-native) and substantially reduced numbers of germinants. The reduction varied with species depending on the proportion of seed present at depth, as described below. Reduced germination was also strongly correlated with the amount of soil heating that occurred where samples were located (Odion and Davis 2000). Thus, the number of post-burn germinants was much greater in samples from gaps vs. under the shrub canopy. Horizontal patterns of seed abundance are analyzed in Odion and Davis (2000).

There were 20 and 31 species that germinated in the field respectively at the two sites (Table 1). Twelve were at both. Four species germinated in the field plots but not seed bank samples. There was only one individual of each. Seventeen species germinated in samples but did not germinate and/or emerge in the field, including species whose seed was among the most abundant (e.g., *Centaurium davyi*, *Mimulus floribundus* Lindley). Another, *Crassula connata*, was virtually absent in the field in the burn areas, although it was common in adjacent unburned chaparral. Field populations for most species were much smaller than post-burn seed bank populations—between ~5 and 14 times smaller for shrubs, and generally even smaller for other species.

Germination treatments. Only two species, both

perennial *Gnaphaliums*, had germination that was not affected by the heat treatment (Table 1). One of these, *G. microcephalum* Nutt. was significantly negatively affected by charate. Among heat-affected species, the two obligate-seeding species of *Ceanothus*, the subshrub *Helianthemum scoparium*, and the annual *Trifolium microcephalum* Pursh had significantly greater germination with heat alone, while the opposite occurred for the annual *Calandrinia ciliata* (Ruíz Lopez & Pavón) DC. (Table 1). Other important species that had a positive response to heat were also affected by charate. *Adenostoma*, *Arctostaphylos purissima*, and *Lotus strigosus* had significantly greater germination with heat and charate compared to heat alone.

Germination of *Centaurium davyi* and *Crassula connata* with heat and charate was not only significantly lower than with heat alone, but also lower than with no treatment. *Crassula* was rare in the burn areas, and *Centaurium* did not occur there until the third year after fire. Both species were fairly common in the surrounding unburned chaparral. *Mimulus floribundus* had much lower germination with heat and charate than with heat alone, but heat and charate germinants outnumbered those in control samples ($P > 0.05$, NS). This species, though abundant in several samples, was absent from most. It was never observed in the field, including in unburned chaparral. It is typically found in seasonal wetlands like two other species that were found in samples, but not in the field, *Crassula aquatica* (L.) Schönl. and *Centunculus minimus* L.

With a relatively high proportion of seed at depth (76 percent below 2.5 cm in gap, edge, and understory samples combined, Table 2), *Arctostaphylos purissima* had better survival (post-burn/pre-burn = 17 percent) than *Adenostoma* (site 1 = 2 percent, site 3 = 3 percent) which only had 22 percent of its seed below 2.5 cm. These survival percentages are from transect samples. The 2.5–7.5 cm depth samples had relatively little emergence of species with charate-enhanced germination. Seeds of other shrubs were not abundant enough to evaluate depth distribution. The high survival of *Ceanothus cuneatus* at site 2 (33 percent) as well as results from a fuel translocation experiment (Odion and Davis 2000) suggest this obligate-seeder had a high proportion of seed at depth.

Helianthemum scoparium was particularly abundant and not affected by charate, so the effect of the depth distribution of its seed is relatively clear. The subshrub had 53 and 75 percent of its seed bank below 2.5 cm in gap and understory samples respectively. Despite the greater proportion of seed at depth at understory plots, survival was similar there (22 percent) compared to gaps (24 percent). Survival along the site 1 transect was 9 percent (post-burn/pre-burn heat). After fire, 94 percent of *Helianthemum scoparium* seeds were below 2.5 cm in the soil in understory plots, only half were at depth in gap plots.

TABLE 1. NUMBER OF GERMINANTS, EXPRESSED AS DENSITY PER M², EMERGING FROM 47 SEED BANK SAMPLES, INCLUDING ALL THREE PRE-BURN TREATMENTS (FIRST THREE COLUMNS). + indicates a significant positive heat effect, ++ indicates a significant positive charate effect, - indicates negative effect (P < .05, Kruskal-Wallis rank sum test). Emergence from post-burn samples and in the field the first year after fire are shown in columns 4 and 5.

	Site 1					Site 2				
	Control	Heat	Heat and charate	Post-burn	Field	Heat and charate	Post-burn	Field		
SHRUBS										
<i>Artemisia californica</i>	0	0	0	0	0	259.6	4.4	.04		
<i>Adenostoma fasciculatum</i>	140.8	246.4 ⁺	738.5 ⁺⁺	17.6	2.1	633.6	17.6	0.2		
<i>Arctostaphylos purissima</i>	30.8	180.4 ⁺	290.4 ⁺⁺	48.4	3.3	0	4.4	0		
<i>Baccharis pilularis</i>	13.2	8.8	8.8	0	0.1	44.0	0	0		
<i>Ceanothus cuneatus</i>	0	35.2 ⁺	30.8	0	1.6	145.2	48.4	10.1		
<i>Ceanothus impressus</i>	0	39.6 ⁺	57.2	13.2	0.8	0	4.4	.02		
<i>Eriocameria ericoides</i>	22	4.4	0	0	0	0	0	0		
<i>Ribes malvaceum</i>	0	0	0	0	0	0	0	.02		
<i>Salix lasiolepis</i>	0	0	0	0	0	13.2	22.0	0		
<i>Salvia mellifera</i>	0	0	0	0	0	74.8	4.4	66.0		
SUBSHRUBS										
<i>Carpobrotus edulis</i>	17.6	35.2	8.8	0	0.1	0	0	0		
<i>Eriophyllum confertiflorum</i>	0	0	0	0	0	88.0	0	.06		
<i>Helianthemum scoparium</i>	114.4	1689.6 ⁺	1346.4	118.8	6.0	6859.6	1456.4	45.0		
<i>Horkelia cuneata</i>	0	4.4	0	0	0	8.8	13.2	26.4		
<i>Lotus scoparius</i>	0	0	0	0	0	382.8	57.2	3.7		
<i>Mimulus aurantiacus</i>	0	0	0	0	0	875.6	30.8	0		
<i>Solanum douglasii</i>	0	0	0	0	0	8.8	0	.02		
<i>Solanum xanti</i>	0	0	0	0	0	4.4	0	.02		
PERENNIAL HERBS										
<i>Carex globosa</i>	4.4	26.4	8.8	4.4	0.1	4.4	0	74.8		
<i>Gnaphalium canescens</i>	4.4	13.2	0	0	0	0	0	0		
<i>Gnaphalium microcephalum</i>	118.8	198.0	35.2 ⁻	0	0	74.8	4.4	0		
<i>Gnaphalium ramosissimum</i>	127.6	136.4	105.6	22	0	1258.4	52.8	.02		
<i>Melica imperfecta</i>	0	0	0	0	0	4.4	0	0		
<i>Mimulus floribundus</i>	118.8	743.6	250.8	0	0	0	44.4	0		
<i>Nassella lepida</i>	4.4	22	0	4.4	0	0	0	0		
ANNUALS										
<i>Anagallis arvensis</i>	0	0	0	0	0	83.6	4.4	.15		
<i>Anthemis cotula</i>	0	0	4.4	0	0	0	0	0		
<i>Aphanes occidentalis</i>	0	0	0	0	0	13.2	0	0		
<i>Aptastrum angustifolium</i>	8.8	79.2 ⁺	57.2	0	1.2	39.6	0	3.4		
<i>Calandrinia ciliata</i>	110	39.6 ⁻	26.4	0	0	57.2	0	0		
<i>Calyptridium monandrum</i>	4.4	8.8	0	0	0.1	127.6	17.6	.02		
<i>Camissonia micrantha</i>	0	0	0	0	0	105.6	22.0	.04		
<i>Centaureum davyi</i>	567.6	1355.2 ⁺	365.2 ⁻	52.8	0	3049.2	444.4	0		
<i>Centunculus minimus</i>	22	167.2 ⁺	17.6	0	0	0	0	0		
<i>Chorizanthe diffusa/angustifolia</i>	30.8	61.6	30.8	8.8	0.02	22.0	4.4	.15		
<i>Conyza canadensis</i>	0	70.4	8.8	8.8	0	0	0	0		
<i>Crassula aquatica</i>	0	4.4	0	0	0	0	0	0		

TABLE 1. CONTINUED.

	Site 1				Site 2			
	Control	Heat	Heat and charate	Post-burn	Field	Heat and charate	Post-burn	Field
<i>Crassula connata</i>	2094.4	3159.2+	859.8-	228.8	0.2	981.2	347.6	0
<i>Cryptantha clevelandii</i>	0	0	8.8	0	0	114.4	0	0
<i>Cryptantha micromeres</i>	0	0	0	0	0	44.4	4.4	.02
<i>Daucus pusillus</i>	4.4	57.2	17.6	0	0	572.0	127.6	1.5
<i>Epilobium adenocaulon</i>	0	0	0	0	0	4.4	0	0
<i>Eucripta chrysanthemifolia</i>	0	0	0	0	0	17.6	0	.09
<i>Filago arizonica</i>	8.8	4.4	4.4	0	0	17.6	0	0
<i>Filago californica</i>	8.8	4.4	0	0	0	61.6	8.8	0
<i>Filago gallica</i>	26.4	52.8	26.4	0	0.1	26.4	0	0
<i>Gastridium ventricosum</i>	4.4	0	0	0	0	0	4.4	0
<i>Gnaphalium purpureum</i>	114.4	325.6+	453.2++	0	0	79.2	0	0
<i>Guillemia lasiophyllum</i>	0	0	0	0	0	4.4	0	0
<i>Hypochoeris glabrata</i>	8.8	8.8	0	0	0	13.2	4.4	.02
<i>Juncus bufonius</i>	13.2	61.6+	8.8	0	0	13.4	17.6	0
<i>Juncus sphaerocarpius</i>	8.8	17.6	4.4	4.4	0	0	0	0
<i>Linaria canadensis</i>	48.4	57.2	17.6	0	0.1	250.8	52.8	.06
<i>Lotus hamatus</i>	8.8	30.8+	79.2	13.2	0	8.8	13.4	0
<i>Lotus salsgingosus</i>	4.4	158.4+	39.6-	17.6	2.5	0	0	0
<i>Lotus strigosus</i>	17.6	343.2+	457.6++	26.4	1.3	167.2	26.4	3.7
<i>Melilotus indicus</i>	0	0	0	0	0	0	0	.02
<i>Microseris lindleyi</i>	0	4.4	0	0	0	0	0	0
<i>Navarretia atractylloides</i>	352	585.2+	734.8	180.4	5.2	721.6	79.2	.6
<i>Pectocarya penicillata</i>	0	0	0	0	0	57.2	8.8	0
<i>Polycarpon depressum</i>	0	0	0	0	0	57.2	8.8	.02
<i>Polypogon monspeliensis</i>	4.4	0	0	0	0	0	0	0
<i>Psilocarphus tenellus</i>	0	0	0	0	0	4.4	0	0
<i>Pterostegia drymaroides</i>	0	0	0	0	0	57.2	0	.02
<i>Sagina decumbens</i>	0	0	4.4	0	0	0	0	0
<i>Senecio californica</i>	0	0	0	0	0	4.4	0	0
<i>Silene gallica</i>	0	0	0	0	0	4.4	0	0
<i>Silene multinervia</i>	4.4	0	0	0	0.1	0	0	0
<i>Spergularia maritima</i>	0	0	0	0	0.1	0	0	0
<i>Stylocline gnaphalioides</i>	13.2	0	0	0	0	0	0	0
<i>Trifolium microcephalum</i>	4.4	167.2+	110	0	0	8.8	0	0
<i>Triodanis biflora</i>	0	0	0	0	0	0	12.2	0
<i>Vulpia microstachys</i>	0	8.8	4.4	0	0	44.4	0	0
<i>Vulpia octoflora</i>	4.4	74.8+	74.8	8.8	0.1	492.8	101.2	.5
Unidentified grass	0	0	0	0	0	0	0	.02

TABLE 2. NUMBERS OF GERMINANTS, EXPRESSED AS AVERAGE NUMBER PER M², FROM 0–2.5 CM AND 2.5–7.5 CM DEPTH FRACTIONS BEFORE AND AFTER FIRE, AND IN THE FIELD FROM THE SAME PLOTS IN WHICH THE SEPARATE DEPTH SAMPLES WERE TAKEN. Values are the averages from 30 samples expressed as the density of seed per m². Pre-burn samples were treated with heat and charate.

	pre-burn		post-burn		field
	0–2.5	2.5–7.5	0–2.5	2.5–7.5	
SHRUBS					
<i>Adenostoma fasciculatum</i>	240.1	52.92	53.9	8.8	5.4
<i>Arctostaphylos purissima</i>	44.1	141.1	36.8	26.5	10.6
SUBSHRUBS					
<i>Helianthemum scoparium</i>	411.6	582.6	88.2	145.6	47.0
PERENNIAL HERBS					
<i>Mimulus floribundus</i>	1519.0	538.0	39.2	26.5	0
ANNUAL HERBS					
<i>Apiastrum angustifolium</i>	245.0	26.5	0	17.6	0.8
<i>Centaurium davyi</i>	1396.5	608.6	558.6	185.2	0
<i>Crassula comata</i>	6056.4	1525.9	1166.2	493.9	1.6
<i>Cryptantha clevelandii</i>	78.4	17.6	0	0	0.1
<i>Lotus strigosus</i>	83.3	88.2	19.6	79.4	11.0
<i>Navarretia atractyloides</i>	3013.5	299.9	274.4	61.7	29.7

Survival percentages of the seed bank for species whose germination was negatively affected by charate are equivocal because post-burn samples presumably contained the inhibitors(s). Among the remaining annuals, high mortality was common. In fact, *Apiastrum angustifolium* Nutt. though fairly common in pre-burn samples, was not detected in post-burn transect samples, and was rare in the field. Seed of this diminutive plant was predominantly near the surface (Table 2). The second most abundant species in the field after fire was the annual *Navarretia atractyloides*. Combining data from gap and understory plots in Table 2, while better illustrating survival at depth, obscured other patterns. Where seed of this species was concentrated, in canopy gap areas, only 6 percent of its seed was below 2.5 cm in the soil, explaining why only 10 percent survived there despite relatively low soil heating with fire. Conversely, in the understory, 16 percent of seed was in the deeper fraction, explaining the relatively high survival (22 percent) along the site 1 transect (predominantly understory). Seed of *Lotus strigosus* (Nutt.) E. Greene was equally abundant in deep and shallow samples overall (Table 2). Survival in surface samples was a relatively high 24 percent, and at depth 90 percent.

DISCUSSION

My procedures indicated that seed mortality with fire was substantial, and greater in the older stand. Previous studies have also found that a significant number of seeds do not survive fire in chaparral (Keeley 1977; Davey 1982; Bullock 1982; Zammit and Zedler 1988; Davis et al. 1989). For species to ensure successful recruitment after fire, their seeds must accumulate at depths in the soil where they will be safe. There must be strong resistance to ger-

mination in the absence of fire for this to occur. Consistent with this, I found that most of the seed bank for many species needed fire to germinate (Table 1). Two shrubs, both species of *Ceanothus*, had germination that was entirely fire-dependent. However, I also found that a small but distinct portion of the seed bank for all other fire-recruiters germinated with simply moisture and natural temperature fluctuations. In addition, there were no short-lived species detected that had entirely fire-dependent germination (i.e., there were no specialized fire annuals), which is not typical for chaparral. Seedlings of these are usually found only the first year after fire (Keeley et al. 1981). Short-lived species in my study all produced seedlings after the first post-fire growing season (Odion 1995, unpublished data). Thus, fire-recruiters in this study, other than *Ceanothus*, produce seed that is both refractory and not. Based on my germination results and those by Davis et al. (1989) and Holl et al. (2000), as well as extensive field observation (Davis et al. 1988; Odion et al. 1992; Odion et al. 1993) non-refractory seed may be somewhat more important in maritime vs. inland chaparral, at least among short-lived species. Conversely, for *Adenostoma*, the proportion of non-refractory seed (19%, Table 1) is in agreement with what has been found at more inland locations (Stone and Juhren 1953; Zammit and Zedler 1988).

How might having seed that is both refractory and not be a selective advantage in chaparral? By producing seed that germinates readily in the field, short-lived species may grow and reproduce throughout the fire cycle, which may be critical for them to sustain seed populations from one fire to the next (Zammit and Zedler 1988). As fire interval increases, the capability to augment the seed bank between fires will be of increasing importance to short-lived species because their seed banks will

otherwise diminish due to mortality and predation. Therefore, considering the past likelihood of relatively long fire intervals in maritime chaparral, it is not surprising that I found non-refractory seed to be so prevalent, even among fire-recruiters. It is possible that some non-refractory seed remains dormant under the chaparral canopy due to inhibitors. However, short-lived species such as *Navaretia atractyloides*, *Helianthemum scoparium*, *Chorizanthe* spp. and *Camissonia micrantha* (Sprengel) Raven are common in old age class maritime chaparral (Davis et al. 1988; Holl et al. 2000), particularly in the canopy gaps that typify this vegetation. Their seeds are concentrated in gaps, an advantage because survival with fire is much greater there (Odion and Davis 2000). The germination ecology of these and other short-lived species allows them to exploit gaps when they appear in maritime chaparral, resulting in more abundant post-fire recruitment than would otherwise occur. Such opportunistic germination has been documented in other chaparral (Zammit and Zedler 1988), and linked to canopy gaps (Shmida and Whittaker 1981), but its relative importance undoubtedly varies with chaparral canopy dynamics.

The dominant shrubs in the study, *Adenostoma*, *Arctostaphylos*, and the two species of *Ceanothus*, are fire-recruiters. Nearly all chaparral areas are dominated by some combination of these genera and there has been much interest in their germination ecology. For *Adenostoma*, the most widespread and abundant chaparral shrub, a question that has persisted had been, what is the role of heat in germination of refractory seed? *Adenostoma* seed banks have been studied previously by Christensen and Muller (1975) who heated soil under shrubs *in situ* Zammit and Zedler (1988, 1994) who burned straw over soil placed in flats, and Parker (1987) who oven-heated soil and supplied charred wood extract. The first two procedures enhanced germination of *Adenostoma*, but it is unclear whether this was a direct or indirect effect of heat. Parker (1987) found that charred wood extract, not heat, enhanced germination. It is possible that the heat he supplied (100°C for 1 h) was in excess of what the seeds in the samples could tolerate since it resulted in a decrease in germination. On seeds collected from shrubs, oven-heating stimulated germination (Wright 1931; Sampson 1944; Stone and Juhren 1953). In addition, Keeley (1987) found that heat alone increased germination compared to controls in 6 of 6 different temperature treatments, but there was not a statistically significant effect. However, Keeley did find significantly enhanced *Adenostoma* germination with charate, and that there was a synergistic effect with heat and charate. I also found that heat and charate produced a synergistic effect, but unlike Keeley, that germination was significantly enhanced with heat alone. It is possible that stimulatory substances were formed and/or inhibitors destroyed when I heated soils. Chemical stim-

ulants can be produced when soil or wood are heated to 175°C for 10–30 min (Keeley and Nitzberg 1984; Keeley and Pizzorno 1986). However, these stimulants are effective in very low concentrations (Keeley and Pizzorno 1986) and my heat treatment did not produce a germination effect comparable to that found with heat and charate.

In contrast to *Adenostoma*, the *Arctostaphylos* and *Ceanothus* spp. in this study are narrowly distributed taxa whose germination ecology has not been previously studied. However, congeneric ecological analogs can be compared. I found that heat was effective in inducing *Arctostaphylos purissima* seeds to germinate, and again that there was a synergistic effect with both heat and charate. This effect has been found in one other *Arctostaphylos* that coincidentally is also a narrow endemic from maritime chaparral, *A. morroensis* Wiesel. & B. Schreiber (Tyler et al. 1998; Tyler et al. 2000). Their methods avoided potential influence of soil-derived stimulants because seeds were extracted from the soil prior to heating. Germination doubled with heat and charate, but, there was no effect with heat alone, or charate alone. Conversely, Parker (1987) found that dormancy of *A. canescens* seeds extracted from the soil was overcome by charred wood extract alone. Freshly collected seed remained dormant with the same treatment. Other research using freshly collected seed has found that just heat (Sampson 1944; Berg 1974) or charate (Keeley 1987) can be effective in breaking seed dormancy of *Arctostaphylos*. Further research on *Arctostaphylos* spp. seed banks is needed to determine how variation in their germination may be correlated with fire regime or other environmental variables.

Ceanothus spp. have a hard seed coat that can be cracked by heat (Quick 1935; Quick and Quick 1961). There can be some germination in the absence of fire if the impermeability of the seed coat deteriorates over time (Quick and Quick 1961), e.g., *C. greggi* A. Gray, (Moreno and Oechel 1991; Zammit and Zedler 1994). In addition, Keeley (1991) reports that it is typical for a few percent of the seeds of *Ceanothus* to be non-refractory. In the stands I studied, seeds of *C. cuneatus* var. *fascicularis* and *C. impressus* had resided in the soil for a considerable length of time. Neither species was in the pre-burn vegetation in the older stand; both drop out as stands of maritime chaparral age—after only ~20 y in the case of *C. impressus* (Davis et al. 1988). Nonetheless, I found no germination of this species or *C. cuneatus* var. *fascicularis* without heat. Because input into the seed bank for these species will cease in long-unburned stands, seeds must survive and remain dormant for their seed banks to persist. These two species may have seed coats that are especially resistant to deterioration, perhaps because they are relatively thick. Thickness of seed coats is correlated with heat endurance (Wright 1931), and I found these *Ceanothus* spp. were more capable of germinating in areas of great-

er soil heating than any other species at the two burn sites (Odion and Davis 2000).

Another hard-seeded species with heat-stimulated germination was the annual *Lotus strigosus* (Table 1). It is curious that this species, unlike the *Ceanothus* spp., had germination further enhanced by heat and charate. *Lotus strigosus* was common the second spring after fire. Second year plants may have emerged from seed that did not germinate the first year, or from seed produced the first year. Charate-induced germination could allow newly produced seed to germinate the following year without heat if water soluble byproducts of wood combustion are still present in the burn area. Another hard-seeded annual legume *Trifolium microcephalum* did not have charate-enhanced germination, and the phenomenon has not been reported among other hard-seeded species (Baskin and Baskin 1998; Table 10.6).

Baskin and Baskin (1998; Tables 10.4 and 10.7) list a few chaparral species that may have germination reduced by heat or charred wood extracts. I found germination that was suppressed by heat (one species), and by heat and charate (three species; Table 1). Curiously, two of the species suppressed by heat and charate (*Crassula connata* and *Centaurium davyi*) had germination that was enhanced by heat alone. Both were uncommon in the field after fire despite having abundant seed in the soil. In fact, it was not until three to four years after each burn that *Centaurium* seedlings appeared, so the same mechanism that inhibited germination in samples apparently operated in the field. The results for *Crassula* may be at odds with what occurs elsewhere. This species is often apparent after fire in chaparral, however, this may be due to increased biomass of individuals, not increased densities.

In conclusion, seed banks in the maritime chaparral I studied may differ from most inland counterparts in the following ways: 1) greater importance of non-refractory seed, 2) lack of entirely fire-dependent germination in short-lived species, 3) germination among *Arctostaphylos* stimulated by heat and especially heat and charred wood extracts together, 4) more strongly enforced dormancy among *Ceanothus* spp. and 5) greater importance of fire-suppressed germination. Conversely, germination of the *Adenostoma* seed bank appears consistent with what occurs elsewhere. Further study of soil seed banks will be required to determine whether there has in fact been divergence in the germination ecology of maritime chaparral. In particular, it would be illuminating to directly compare seed banks of species that occur in both inland and maritime chaparral.

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LITERATURE CITED

- AULD, T. D. AND M. A. O'CONNELL. 1991. Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* 16:53-70.
- BASKIN, C. C. AND J. M. BASKIN. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, CA.
- BERG, A. R. 1974. *Arctostaphylos* Adans. manzanita. Seeds of woody plants in the United States, USDA Forest Service.
- BOND, W. J. AND B. W. VAN WILGEN. 1996. Fire and plants. Chapman and Hall, New York, New York.
- BORCHERT, M. I. AND D. C. ODION. 1995. Fire intensity and vegetation recovery in chaparral: a review, p 91-100. in J. E. Keeley, and T. Scott (eds.), *Brushfires in California: ecology and resource management*. International Association of Wildland Fire, Fairfield, WA.
- BULLOCK, S. H. 1982. Reproductive Ecology of *Ceanothus cordulatus*. M. A. Thesis, California State University, Fresno.
- CHRISTENSEN, N. L. AND C. H. MULLER. 1975. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. *Ecological Monographs* 45:29-55.
- D'ANTONIO, C. M., D. C. ODION AND C. M. TYLER. 1993. Invasion of maritime chaparral by the alien succulent *Carpobrotus edulis*: the roles of fire and herbivory. *Oecologia* 95:14-21.
- DAVEY, J. R. 1982. Stand Replacement in *Ceanothus crassifolius*. M.S. Thesis, California State Polytechnic University, Pomona.
- DAVIS, F. W., D. E. HICKSON AND D. C. ODION. 1988. Composition of maritime chaparral related to fire history and soil, Burton Mesa, California. *Madroño* 35:169-195.
- , M. I. BORCHERT AND D. C. ODION. 1989. Establishment of microscale vegetation pattern in maritime chaparral after fire. *Vegetatio* 84:53-67.
- DIBBLEE, T. W. 1950. Geology of southwestern Santa Barbara County. Bulletin 150, California Division of Mines, Sacramento.
- EMERY, D. 1988. Seed Propagation of Native California Plants. Santa Barbara Botanic Garden, Santa Barbara, California.
- GRIFFIN, J. R. 1978. Maritime chaparral and endemic shrubs of the Monterey Region, California. *Madroño* 25:65-81.
- HICKMAN, J. C. (ed.). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley.
- HOLL, K. D., H. N. STEELE, M. H. FUSARI AND L. R. FOX. Seed banks of maritime chaparral and abandoned roads: potential for vegetation recovery. *Journal of the Torrey Botanical Society* 127:207-220.
- KAMINSKY, R. 1981. The microbial origin of the allelopathic potential of *Adenostoma fasciculatum* H. & A. *Ecological Monographs* 51:365-382.
- KEELEY, J. E. 1975. Longevity of nonsprouting *Ceanothus*. *American Midland Naturalist* 93:505-507.
- . 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric

- pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58:820–829.
- . 1984. Factors affecting germination of chaparral seeds. *Bulletin of the Southern California Academy of Sciences* 83:113–120.
- . 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68:434–444.
- . 1991. Seed germination and life history syndromes in the California chaparral. *The Botanical Review* 57:81–116.
- . 1992. Demographic structure of California chaparral in the long-term absence of fire. *Journal of Vegetation Science* 3:79–90.
- . 1993. Utility of growth rings in the age determination of chaparral shrubs. *Madroño* 40:1–14.
- , AND M. NITZBERG. 1984. The role of charred wood in the germination of the chaparral herbs *Emmenanthe penduliflora* (Hydrophyllaceae) and *Eriophyllum confertiflorum* (Asteraceae). *Madroño*, 208–218.
- , B. A. MORTON, A. PEDROSA AND P. TROTTER. 1985. The role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. *Journal of Ecology* 73:445–458.
- , AND C. J. FOTHERINGHAM. 1997. Trace gas emissions and smoke-induced seed germination. *Science* 276:1248–1250.
- , AND ———. 1998. Smoke-induced seed germination in California chaparral. *Ecology* 79:2320–2336.
- KEELEY, S. C., J. E. KEELEY, S. M. HUTCHINSON AND A. W. JOHNSON. 1981. Postfire succession of the herbaceous flora in southern California chaparral. *Ecology* 62:1608–1621.
- , AND M. PIZZORNO. 1986. Charred wood stimulated germination of two-fire following herbs of the California chaparral and the role of hemicellulose. *American Journal of Botany* 73:1289–1297.
- KEITH, D. A. 1987. Combined effects of heat shock, smoke and darkness on germination of *Epacris stuartii* Stapf., an endangered fire-prone Australian shrub. *Oecologia* 112:340–344.
- MCPHERSON, J. K. AND C. H. MULLER. 1969. Allelopathic effects of *Adenostoma fasciculatum*, ‘chamise’, in the California chaparral. *Ecological Monographs* 39:177–198.
- MORENO, J. M. AND W. C. OECHEL. 1991. Fire intensity effects on germination of shrubs and herbs in southern California chaparral. *Ecology* 72:1993–2004.
- MULLER, C. H., R. B. HANAWALT AND J. K. MCPHERSON. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. *Bulletin of the Torrey Botanical Club* 95:225–231.
- ODION, D. C. 1995. Effects of variation in soil heating during fire on patterns of plant establishment and regrowth in maritime chaparral. Dissertation, University of California, Santa Barbara.
- , AND F. W. DAVIS. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs* 70:149–169.
- , D. E. HICKSON, AND C. M. D’ANTONIO. 1992. Central coast maritime chaparral on Vandenberg air force base: an inventory and analysis of management needs for a threatened vegetation association. Report prepared for The Nature Conservancy.
- , J. STORRER AND V. SEMONSEN. 1993. Biological resources assessment, Burton Mesa Project Area, Santa Barbara County, California. Report prepared for Santa Barbara County, Resource Management Department.
- PARKER, V. T. 1987. Effects of wet-season management burns on chaparral vegetation: implications for rare species. Pp. 233–237. in T. S. Elias and J. Nelson (eds.), *Conservation and management of rare and endangered plants*. California Native Plant Society, Sacramento.
- , AND V. R. KELLY. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. Pp. 231–255. in M. A. Leck, V. T. Parker and R. L. Simpson (eds.), *Ecology of soil seed banks*. Academic Press Inc., San Diego, CA.
- QUICK, C. R. 1935. Notes on the germination of *Ceanothus* seeds. *Madroño* 3:135–140.
- , AND A. S. QUICK. 1961. Germination of *Ceanothus* seeds. *Madroño* 16:23–30.
- SAMPSON, A. W. 1944. Plant succession on burned chaparral lands in northern California. University of California Agricultural Experiment Station Bulletin 685.
- SHMIDA, A. AND R. H. WHITTAKER. 1981. Pattern and biological microsite effects in two shrub communities, Southern California. *Ecology* 62:234–251.
- STONE, E. C. AND G. JUHREN. 1951. The effects of fire on the germination of the seed of *Rhus ovata* Wats. *American Journal of Botany* 38:368–372.
- , AND ———. 1953. Fire stimulated germination. *California Agriculture* 7:13–14.
- SWEENEY, J. R. 1956. Responses of vegetation to fire. University of California Publications in Botany 28:143–250.
- SWANK, S. E. AND W. C. OECHEL. 1991. Interactions among the effects of herbivory, competition, and resource limitation on chaparral herbs. *Ecology* 72: 104–115.
- THANOS, C. A. AND P. W. RUNDEL. 1995. Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* 83:207–216.
- TYLER, C. M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83:1009–1020.
- , D. C. ODION AND D. MEADE. 1998. Ecological studies of Morro Manzanita (*Arctostaphylos morroensis*), seed ecology and reproductive biology. Report prepared for California Department of Fish and Game, Species Conservation and Recovery Program.
- , ———, ——— AND M. A. MORITZ. 2000. Factors affecting regeneration of Morro Manzanita (*Arctostaphylos morroensis*): reproductive biology and response to prescribed burning. Report prepared for the California Department of Fish and Game, Species Conservation and Recovery Program.
- WELLS, P. V. 1969. The relation between mode of reproduction and extent of speciation in the woody genera of the California chaparral. *Evolution* 23:264–267.
- WICKLOW, D. T. 1977. Germination response in *Emmenanthe penduliflora* (Hydrophyllaceae). *Ecology* 58: 201–205.
- WHELAN, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge, Great Britain.
- WRIGHT, E. 1931. The effect of high temperature on seed germination. *Journal of Forestry* 29:679–687.
- ZAMMIT, C. A. AND P. H. ZEDLER. 1988. The influence of dominant shrubs, fire and time since fire on soil seed banks in mixed chaparral. *Vegetatio* 75:175–187.
- , AND P. H. ZEDLER. 1994. Organisation of the soil seed bank in mixed chaparral. *Vegetatio* 111:1–16.